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THE INTESTINE OF THE MINNOW CAMPOSTOMA ANOMALUM (RAFINESQUE), WITH SPECIAL REFERENCE TO THE DEVELOPMENT OF ITS COILING.*

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CONTENTS.

I. INTRODUCTION.

Fishes of the genus *Campostoma* (Cyprinidæ) are characterized by an intestine which is coiled around the air bladder, a structural peculiarity found in no other known fishes. At the suggestion of Professor R. C. Osburn the writer undertook a study of the development, in post-embryonic life, of this intestinal coiling in *Campostoma anomalum* (Rafinesque), and the anatomy of such parts of the canal as would be essentially involved in this general problem.

During the summers of 1920 and 1921, when the writer was a member of a state fish survey party under Dr. Osburn, for the

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Ohio Division of Fish and Game, very many of this species were taken with the seine in various Ohio waters. Some were contributed by a small field party of 1922, and during the same spring and summer the writer collected numerous, mostly young specimens in creeks in the vicinity of Columbus. A total of 600 specimens were studied.

The writer wishes to express his indebtedness to Prof. R. C. Osburn, Head of the Department of Zoology and Entomology, Ohio State University, who gave valuable aid and suggestions; to Mr. Carl L. Hubbs, Curator of fishes, Museum of Zoology, University of Michigan, for help in determination of immature specimens, to a number of Ohio State colleagues who helped with the seine, and to his wife for the averaging of hundreds of fish measurements to get final data in table 2.

II. Anatomy of the Intestine.

(*A*) *General Structure.*

The intestine in *Campostoma* adults appears to be a closely wound spiral, which surrounds other parts of the digestive system and the air bladder, (Plate VI, Fig. 67). However, a small anterior portion of the air bladder is not dorsally covered in any specimens, though it had previously been described (Jordan and Evermann, 1896, p. 204) as "entirely surrounded by many convolutions of the long alimentary canal."

The intestine length is not remarkable for other Cyprinidæ which are essentially vegetable feeders or limophagous, have a long intestine. In *Pimephales promelas* it is as long as in *Campostoma.* Coiling necessarily occurs in various groups of vertebrates, wherever a lengthy intestine exists; but only in this one genus is there a transverse coiling, passing intestinal loops dorsally over air bladder.

Gonads are not enclosed within intestinal coils, (Plate VII, Fig. 100), though they have been described as thus enclosed, (Jordan and Evermann, 1896, p. 294). The relation of gonads to canal is discussed in a later part of this paper.

In a small percentage of cases all dorsal intestinal loops are lacking, the air bladder being completely exposed dorsally. These thus show no conformity to the intestinal arrangement used as the first diagnostic character in classification keys.

The oesophagus in *Campostoma*, as in other fishes, is a short tube, scarcely projecting posteriorly into the coelom. Anteriorly it widens into pharynx. Posteriorly it widens out into the thickest part of the canal, from which to be sure it is not separated by any constriction. The oesophagus itself was not studied.

The thickest part of the alimentary canal, the apparent stomach, (the nature of which will be discussed below) has a diminution in diameter posteriorly. The canal passes with a very pronounced, sharp bend, at the posterior end of the abdominal cavity, into the long intestine, but with no pyloric valve or any other constriction. The intestine is small and of practically uniform diameter throughout, except near the anus, where it tapers down somewhat more. There is no large intestine.

In the very young *Campostoma* the canal is short and simple, consisting (between oesophagus and anus) of three straight portions bent upon each other like parts of a flattened letter Z. The comparison to a letter Z is distinctly better in this case than the letter S, sometimes used in such alimentary canal descriptions. At first all of the first or anterior of the three canal parts, the thickest of the three, was thought of as stomach. The adult intestinal condition is the result of an extensive coiling process during growth, principally of the middle and end parts of the Z-shaped canal.

(*B*) *Detailed Study of the Intestine With Special Reference to Absence of Stomach and Nature of Mucosa Surface.*

Of the original three-part alimentary canal seen in coelom in youngest free-swimming fish, it was first thought (as already suggested), that all of the first, or anterior enlarged part was stomach, and the other parts intestine, but examination demonstrated such demarcation impossible, and raised new questions.

The same interesting problem has been considered in many other Cyprinidæ, all European. The condition described below for Campostoma will be clarified by noting first the prevalence of similar conditions in other minnows, as indicated in the literature.*

*Papers which are probably the most important on both histological and physiological treatment of alimentary canal of minnows are listed in the bibliography.

Yung (1899) summarized and discussed previous work, from which it appears that Bischoff (1838) concluded a stomach properly speaking was lacking in a number of Cyprinidæ. Valatour (1861), Luchhau (1876), Edinger (1877), and others contributed materially to the evidence. Oppel (1896–97) summarized all existing information comprehensively. Pictet (1909) added careful histological work on several species, and reviewing literature, made adequate generalization of the very uniformly accepted conclusions. Part of his summary is quoted here in translation. (Pictet, 1909, pp. 52, 55, 56).

"The intestine properly so-called of the Cyprinoid fishes directly follows the oesophagus, and there is no stomach in the histological sense of the word."

"* * * their intestine * * * continues to the anus without morphological differentiation other than the enlargement of the anterior part."

"The principal reasons which have been given in favor of this view are the following: (1) Complete absence of gastric glands in the swollen part of the digestive tube. It is known that in fishes pepsin glands exist only in the stomach. (2) The fact that the hepatic duct opens, in the stomach-less fishes, 2 or 3 mm. from the oesophagus, while in general it is back of the stomach and opens into the anterior part of the mid-intestine."

"To these arguments which in themselves suffice to show that the swollen part of the intestinal tract should be considered not as stomach, but as anterior portion of the intestine, we can add the following: (3) The mucosa of the stomach of fishes is generally covered with fine folds, while the intestine possesses high, irregular folds; a well defined limit (pyloris) exists between the two parts. But in these fishes large folds appear at the oesophagus and are found to be identical up to the anus, without any demarcation between the swollen part and the rest of the digestive tube."

"(4) There are never any goblet cells in the epithelium of the stomach. In the fishes with which we are concerned, the histology shows us that they occur from the oesophagus to the anus."

"(5) Physiology conforms this view; the reactions of the part in question are in Cyprinidæ alkaline or neutral, as in the intestine of fishes in general, while the reactions of the stomach are most often acid."

"(6) Finally there is no difference between the inner structure of the epithelial cells of the swollen part of the intestine, and that of the cells of the rest of the tube, while in most fishes with differentiated stomach, the cells of the two regions have a different aspect."

In Campostoma, after some development of the alimentary canal, the anterior section of the canal in the coelom, the apparent stomach, becomes differentiated into a more swollen anterior half, having somewhat thicker walls, and a posterior half, remaining less thick. The latter to a small extent does take part in some subsequent coiling, but the anterior does not.

The gall bladder, somewhat difficult to see unless probed for, is joined to the canal by a common bile duct near the mid-point of the entire anterior section, (Plate IV, Fig. 46). Obviously then the thinner posterior half of this long anterior section cannot be stomach.

Still the anterior swollen part, anterior to bile duct, might be stomach, and in older specimens it does look somewhat different than the smaller posterior part. If stomach there would have to be a pyloric valve to separate effectively the acid digestive chamber from the alkaline. There is no indication whatever of pyloris in front of bile duct junction, in any specimens examined. Even if reactions were different the mixing might be but slight because of steady passage of the large mass of canal contents, to prevent appreciable flow anteriorly.

The common bile duct entrance, however, is not quite so far forward as in some other minnows. Of several European species, Edinger (1877) says: "The common bile duct opens at the end of the oesophagus." Valatour (1861) says: "Nearly at the beginning of this swollen part the choleduchal canal opens out." Yung (1899) says: "The choledochal canal enters the intestine immediately behind the oesophagus." In a large *Campostoma* of about 80 mm. length, in which the entire originally anterior canal section was 35 mm. long, nearly 29 mm. preceded the common bile duct junction. This, and other measurements essentially no different, suggest room for a histologically differentiated stomach.

Investigation was briefly made into the nature of the chemical condition in alimentary canal. Parts from freshly stunned specimens were opened. Intestinal contents and scrapings from wall were all used and mashed to free possible digestive juices. In some small specimens where that was impracticable, small parts of the canal were completely mashed and used. In the rather dense intestinal contents no secretions were recognized. Whether specimens in best condition for this purpose were selected could not be determined.

To make the tests a small quantity of mashed substance was placed in white porcelain dish, neutral water added, and drops of the indicator added to the liquid. To what extent the color reactions were of digestive secretions only, rather than also materially of plant substances, etc., is impossible to say. Some better technique must be developed for H ion determination of this particular type.

Since tests gave practically uniform results on material from half a dozen specimens, these may be given here as pertinent at least for conditions worked under. Merely general conclusions seem necessary here. Material for a short distance back of common bile duct junction, showed invariably a weak alkaline reaction. Material from in front of this junction, that is, from the anterior swollen part, showed invariably a very slight acid reaction. It was never quite neutral or alkaline. This acidity, a true stomach property, was unexpected here, in view of the preceding structural evidence of the lack of a true stomach.

The folds of the inner surface of the intestine are conspicuous, especially in the swollen part of the canal. They are on a zig-zag plan, and in superficial view seem quite regular. Oesophagus folds were not examined.

The zig-zag formation has been found in other Cyprinidæ. In these and a few other fishes, there is, according to Edinger (1877), rather than the plan of fully developed crypts of many other Teleosts, "a tendency to the primitive system existing in Cyclostomes, and most Selachii, of simple, lengthwise folds without crypts. Thus the mucosa ridges of *Pleuronectes solea* are arranged one near another without cross connection. They pass in zig-zag direction through the entire intestine."

Pictet (1909, pp. 58, 59), found zig-zag folds in *Cyprinus carpio*, *Carassius auratus*, *Tinca vulgarus*, *Leuciscus rutilis*, and *Barbus fluviatilis*, but there were differences in detail according to species, and in one at least according to age; but he found no differences between the swollen part and the thinner intestine following.

The *Campostoma* mucosa surface zig-zags are similarly unbroken ridges, (Plate VII, Figs. 94, 95). They are not as irregular as in the so-called herring bone weave pattern pictured by Breder and Crawford (1922, Figs. 124-126), for *Leuciscus* and *Notropis*. Only occasionally there occurs a break, or anastomosis, or a slight branch. The V-shaped units of neighboring zig-zags in column, more distinctly impress the eye than the long continuous zig-zag ridges separately. The direction of the sides of the Vs is nearly in the circular direction of the canal, or much more transverse than longitudinal. This suggests transverse folds, but a little study shows this to be due wholly to appearance produced by these acute-angled Vs so directed. In other words the ridges and grooves are longitudinal, but pass in very indirect, zig-zag paths.

For detailed study of intestinal mucosa pieces about 3 mm. long were cut from selected places and the circular surface spread out flat. A large portion of such area was drawn with camera lucida.

The wall of the alimentary canal was found rather thin and translucent, except in a few specimens, where it was considerably thicker and opaque, and in which also the folds were more prominent, so that a cross section through intestine in such thick wall in widest canal part, showed grooves to be almost half as deep as the diameter of the free lumen of the canal. But in all typical cases, which included a great majority of all available specimens, the grooves were relatively much shallower. These typical ones are exclusively referred to in this study.

The typical arrangement is seen, (Plate VII, Fig. 95) in the swollen part, anterior to bile duct junction. For a short distance at the very anterior end of this swollen part, the grooves are even a little deeper, (Fig. 94). Any apparent irregularities in this are due entirely to the fact that the ridges being higher are subject to tilting, with formation often of wavy upper edges. The condition exactly as in Fig. 95 is found not only in most of the swollen part, but also for a little distance in back of bile duct junction. A little farther back the ridges become lower and lower, and also narrower. The Vs are smaller. The grooves then are much smaller, but relatively wider.

After considerable decrease in size of Vs, some variable distance posteriorly there is a modification in that the Vs become isolated by dropping out of parts of ridges, (Plate VII, Fig. 96).

Half of the intestine may be like this. Following comes a longer or shorter portion in which the original Vs are broken up so much that merely short bars (portions of the former sides of the Vs) remain. Often quite a number of these in a specimen, instead of being straight, take the form of small wide-angled Vs in the opposite direction from the original larger Vs (Fig. 97). Still farther posteriorly the bars are shortened still more and lie in a general transverse direction. Where this modification exists there is the appearance of transverse folds, but the explanation shows how this peculiar condition is obtained. Finally in all specimens examined, ridges fade out entirely at some short but variable distance in front of the anus, so that at the end the intestine is entirely without mucosa folds.

The similarity of folds directly anterior and posterior to the bile duct junction, instead of the presence of a different set of fine stomach folds (point 3 in Pictet's summary on conditions in Cyprinidæ), shows the lack of a specialized stomach mucosa in *Campostoma*.

No attempt was made to work out the development of the folding of intestinal mucosa during growth of the fish. Adult specimens only were considered in this work.

Further investigation into question of lack of true stomach was made by microscopical examination of epithelium. Considerable difficulty was experienced in getting satisfactory sections. Specimens were practically always rather filled with food and inorganic material, (Kraatz, 1923, p. 276), which are an obstruction to sectioning. From a few specimens successfully cleaned without injuring mucosa, the following parts were sectioned: portion of swollen region, at region of bile duct junction, posterior to that junction, at about the middle of the long intestine, and also nearer the end. Bouin's and Zenker's fixatives were tried, and sections stained with Delafield's haematoxylin and eosin.

Merely a short general treatment of the histological examination of epithelium will be given. There is a regular columnar epithelial layer, one cell layer thick. Cells are practically alike in size and form on all ridges and in grooves, in different parts of intestine, and in different specimens also, despite any differences in size of folds. Moreover, the cells are the same in the swollen part as behind the bile duct entrance, instead of being of a specialized type, as they would in a true stomach, (point 6 in

Pictet's summary). Such epithelium is described by Pictet (1909, p. 57), and more fully by Oppel, (1896, pp. 35, 72).

Goblet cells are present in the columnar epithelium, but do not seem abundant. They are also present in the swollen part, though possibly less numerous there. Since goblet cells are never found in a true stomach, (point 4 in Pictet's summary) this swollen part in *Campostoma* cannot be differentiated from intestine parts following, and therefore cannot be identified as having a true stomach epithelium.

There was no evidence in the swollen canal part in any specimens examined, of the presence of tubular digestive, or pepsin, or gastric glands, with their specialized cells. Such glands are well described in Oppel, (1896, pp. 22, 33, 69). This lack, (point 1 of Pictet's summary) shows likewise that there is no specialized stomach part present in *Campostoma*.

Most of the evidence demonstrates lack of a true stomach in *Campostoma*, for, to summarize, there is a lack of a pyloric valve, a similarity of folds throughout in swollen part and back of bile duct junction, a similarity of epithelial cell structure in those parts, the presence of goblet cells throughout, and the absence of true stomach or gastric glands. Apparent contradictory points, the somewhat more posterior bile duct junction, and some acid reaction of the swollen part, are of less determining value, in comparison with the other positive structural features. Moreover bile duct junction need not be and often is not at the very beginning of an intestine. The fact that there is considerable distance anterior to it, allows room for the presence of acid reaction, which may not interfere with alkaline juices introduced farther down. By what means the acid secretion is produced is not known. But its presence, as long as not deleterious, does not seem remarkable when one considers that the absence of a stomach in this and other Cyprinidæ is probably not primitive, but rather a case of loss of an earlier physiologically differentiated stomach, which conclusion, entertained by Edinger (1876), seems logical when one realizes that most Teleosts have a true stomach. In Cyprinidæ the loss seems to be universal, but in some other groups there are only occasional species which lack a true stomach, (Oppel, 1896, p. 33). It is possible then that the loss is not equally complete in all cases, and that the slight indication of stomach acidity is a vestige in *Campostoma*.

All of the swollen part is therefore considered as part of the intestine in this paper, and all measurements of intestine length to be given are from posterior end of oesophagus to anus.

III. Development of the Intestine.

The alimentary canal very likely begins as a straight tube, but this condition must be of very brief duration in post-embryonic life. The smallest fish obtained, 13 mm. long, already possessed the flattened Z-shaped canal.

Correlation of intestinal development with development of fish as a whole, though desirable, is impossible. Furthermore, since exact age records are not available for collected material, and thus correlation of intestinal development with age impossible, there remains merely the correlation between length of intestine and length of fish. While this is useful, it must be understood that no very close correlation is to be expected.

All specimens were assigned numbers, which are purely accession numbers, having no other significance. Length of fish is given in millimeters to base of tail.

A typical method of intestinal development obtains in by far the largest number of specimens. Definite detailed advances in this development are assumed to represent stages, designated as stage I, II, III, etc., which are figured on Plates I to V, inclusive.

Inasmuch as intestinal arrangement in the smallest available fish is similar to the general adult alimentary tract in many fishes, this study of development in *Campostoma* might in a way be considered a study of development of complex, coiled condition of a long-intestined fish, over the adult condition of a short-intestined carnivorous fish.

Stage I. (Plate I, Figs. 1, 2). The earliest stage of intestinal development has already been sufficiently described as a flattened Z-shape, of which the three sections, anterior, middle and posterior, are to be remembered as basis for the following developments.

Stage II. (Plate I, Figs. 3, 4). A little growth elongating the posterior canal section, results in a downward bend near the anterior end of that posterior section, at (b) in Fig. 3. This initial, downward U-shaped bend leaves in original position adjacent parts of that section, which now appear as upward bends (a) and (c). In subsequent intestinal coiling, curve (a) will persist as a characteristic landmark on the left side.

Stage III. (Plate I, Figs. 5, 6). Downward bend (b) is deeper. There has also been some growth in the middle section of the canal, where there is a slight bend, nearly in the horizontal plane.

Stage IV. (Plate I, Figs. 7–9). More elongation in the U-shaped bend (b) carries its rounded end across ventrally up to the right side. There is new development in the formation of a bend in the middle section, bend (d), which lies outwardly contiguous to or surrounds (b) ventrally, and there is likewise formed in it the bend (e) which pushes in directly inside of bend (c). All these bends are plainly seen in Fig. 8. The contiguous bends (b) and (d) comprise a double U-shaped bend, now already half way up on the right side, and it is this which will have to be followed primarily.

Stage V. (Plate I, Figs. 10–12). Growth carries bend (b-d) up higher on the right. The left side is as in the preceding stage, except that the posterior part, bend (c-e), is projected upward somewhat, so that it is level with the upper edge of the air bladder.

Stage VI. (Plate I, Figs. 13–15). There is no additional growth upward of (a) or (c-e) or of any other place on the left side. Probably nothing in growth processes of intestine itself would prevent growth in this direction, but the liver (Plate VII, Figs. 92, 93), offers mechanical obstruction. It occupies all available space anterior to and above bend (a) and anterior to (c), though not really above (c), and so could hardly be the cause of lack of growth from the left dorsalward posterior to point (c). At any rate all subsequent growth of intestine results in elongation in the other direction, to the right or counterclockwise. At this stage there is but little apparent growth of (b-d), but enough to make these bends more posteriorly directed. At this time the anterior half of the anterior canal section begins to widen a little.

Stage VII. (Plate I, Figs. 16–18; Plate II, Fig. 22). The (b-d) bend has become more elongated posteriorly, with the end twisted around the tip of the air bladder. Fig. 16 shows the inner side of the tip of the (b-d) bend, stippled darker than the nearer left parts of intestine. The anterior canal section begins to elongate a trifle faster than the body as a whole, making a slight curvature in its course.

Stage VIII. (Plate I, Figs. 19-21; Plate II, Fig. 23). The distinctive development is the growth of the (b-d) bend so that for the first time it lies on the dorsal side of the air bladder.

Stage IX. (Plate II, Figs. 24–28). Continued growth of the (b-d) bend has carried it down half way on the left side so that the outer edge of (d) touches the posterior canal section. Thus the posterior part of the air bladder (Figs. 24, 25), is completely covered dorsally, except for a slit left in the loop of the (b-d) bend. Thus the first complete turn around the air bladder is completed.

The anterior canal section has elongated a little, forming a bend in its thinner posterior half, the end of which has passed from the ventral side, up the right, to the level of the upper part of the air bladder.

Stage X. (Plate II, Figs. 29–32). Bend (b-d) has grown over ventrally to the right side, a half a turn counterclockwise beyond stage IX.

The last part of the posterior intestine section, which had previously passed along the left side to the anus, has now elongated so that it passes ventrally, counterclockwise in a half turn to the right, on which side it passes along above the end of bend (b-d) to the anus.

The anterior section of the canal has grown a little, so that its posterior part has come to lie over the posterior tip of the air bladder, after which it continues into the middle canal section.

A small beginning is here formed of what will be later an inner series of coils. This inner, new intestinal bend may be partly visible in a view of the outer coils because it presses out into the open slit in the end of bend (b-d).

Stage XI. (Plate III, Figs. 33–41). The (b-d) bend has grown from the right, across the dorsal surface, and to the upper part of the left side. These new dorsal loops push forward the older loops which had previously covered the posterior part of the air bladder. Some coils tend to be pushed together much, and the first encircling coil at the anterior end is pushed beneath the edge of bend (c-e) on the left side.

The elongating end part of the posterior canal section has formed another half turn counterclockwise, to the left where it passes back to the anus. This part has made one complete counterclockwise turn between stages IX and XI.

The inner growth, seen only on removing outer posterior coils, is an elongation of the posterior part of the anterior section, and of a small adjacent part of the middle section. In most cases, from the position on the upper left margin, a new U-shaped bend, with the growing point indicated by (x), (Plate III, Fig. 38), makes half a turn counterclockwise. The extent of this is shown where intestine coils are unfolded in one plane, (Fig. 37), but in which all essential bends are retained. In a few cases the (x) growth is not quite as long (Fig. 39), and in a few cases (Figs. 40, 41) it has a different form due to different position of the part concerned relative to air bladder.

Stage XII. (Plate III, Figs. 42, 43; Plate IV, Figs. 44–54). The (b-d) bend has grown down from the upper part of the left, across ventrally to the right side. There is a little more crowding of coils anteriorly.

The end part of the posterior section has made another short diagonal bend around to the right side, where it passes to the anus. (Plate IV, Fig. 44). This has completed one full turn from stage X.

The growth of the inner coils is considerable, but there is much variation in the disposition of the (x) bend. Typically the (x) bend has passed from the right across dorsally, then down the left and across ventrally again. (Plate IV, Fig. 47). The (x) bend in growing around practically a full turn, has thus caught up with the (b-d) bend, but there is relatively no more growth, for its periphery is smaller than that of the older, outer bend. One loop of the (x) bend is usually visible in the small opening in the end of the (b-d) bend.

There were found many specimens of this stage with less growth in the inner part, due possibly to the retardative action of the pressure of the outer coils. Representative variations are shown, (Plate IV, Figs. 48–54). The inner growth in Fig. 49 has a crowding up of small loops which do not encircle the air bladder.

There is another peculiarity of coiling in some specimens. (Figs. 52–54). To distinguish this it should be recalled that in all intestinal development, as described, there was from the very first, a pushing around by elongation or growth of the U-shaped bend in a diagonal, spiral, counterclockwise direction. But in this peculiar type, there is a simple spiral turn around the air bladder, in one or a few counterclockwise turns. This condition may be brought about by the separation of the legs of the U at an early stage of the inner growth. A working model of wire and string, on a stick representing air bladder, disclosed how this could come about. Consider the condition in stage X in which the posterior part of the anterior canal section passes from the right across the posterior tip of the air bladder, to the middle intestinal bend. By a twisting or revolving of the anterior section just on this posterior point as a pivot, which is likely due to varying pressure on these parts, this simple spiral is produced during the course of the lengthening of the inner bend, instead of a U-shaped (x) bend being produced.

Not only fish of from 35 to 50 mm. length, but also most of the larger, older specimens, possessed coiling of this development stage XII. This is shown to be an adult condition. Even a few of stage XI intestinal development were adult, showing that the coiling may, but usually does not, stop at that point. In older specimens there is of course increase of actual intestine length, due to regular growth, in correlation with general increase of size of fish. That there is no relative increase of intestine length was seen in comparing ratios of intestine length to body length for all specimens of stage XII. Old large specimens were found to have the same range of ratios as younger ones which had just attained that development. This individual specimen comparison data cannot be given space in this paper. Table 2, summarizing all data, gives necessarily only averages for the series.

Stage XIII. (Plate IV, Fig. 55; Plate V, Figs. 56–59). There are instances in which more coiling does take place. As compared with 105 specimens of the collection which were in stage XII, 31 specimens had definite additional coiling, which also increased the ratio of intestinal length to body length (see table 2). The (b-d) growth has continued, passing up on the right side, and just across the tip of the dorsal side once more, or a half a turn more counterclockwise.

The end part of the posterior canal section likewise elongates, making another bend from the right, across the dorsal, and down diagonally on the left side to the anus. (Plate V, Figs. 56–58).

The inner growth also continues. From the right side, the (x) bend passes up and across the posterior tip of the air bladder, (Plate IV, Fig. 55). The same sort of variations of the inner coils exist as for stage XII.

Conclusion.—The development to stage XII or to XIII, is attained early within the first year of growth, often shortly after the middle of the summer, at which time stage XII fishes seem to average from 35 to 50 mm. in length. If stage XIII is developed this is done immediately without halt. Subsequent to this first summer's intestinal development to either of these stages, there is no further change, except the increase in length and thickness of intestine correlated roughly with increase in size of fish as a whole.

TABLE 1.

Data on specimens selected for illustration of stages in development of intestine.

Stage of Development	Specimen No.	Length of Fish, mm.	Length of Intestine, mm.	Number of times Intestine is longer than Body
I	296	14	12.6	.90
II	299	13	13.1	1.01
III	365	16	18	1.12
IV	314	16	18	1.20
V	367	18.5	29	1.52
VI	383	24	46	1.92
VII	401	26	57	2.19
VIII	396	25	63	2.52
IX	422	28	79	2.82
X	522	36	115	3.19
XI	195	41	165	4.04
XII	151	48	271	5.64
XIII	123	49	293	6.04

Relative to the largest specimens studied, the following data apply directly to the conclusions here made. Of five specimens over 100 mm. in length, (100 to 110 mm.), only two, (100 mm. and 102 mm.) had intestinal development of stage XIII; the others were stage XII. Of four specimens between 90 and 100 mm. in length, none were of stage XIII, all being stage XII. All these were old specimens. It may be mentioned, of course, that none of the specimens secured were of maximum size the species may attain, but since the development process as far as degree of coiling is concerned, ceases so very early, this would be of no importance. Among the total of 31 specimens of stage XIII, there were also a number of small ones, one at 34 mm., one 43 mm., one 49 mm., and at almost all sizes upward to large, old fish.

TABLE 2.

Summary of measurements of specimens arranged according to stages of intestinal development.

Stage of intestinal development	Total number of specimens	Minimum length of fish, mm.	Maximum length of fish, mm.	Average length of fish, mm.	Minimum length of intestine, mm.	Maximum length of intestine, mm.	Average length of intestine, mm.	Minimum ratio [4]	Maximum ratio	Average ratio [5]
I	5	13	15	14.2	12	13	12.6	.87	.93	.90
II	2	13	13	13	12.1	13.1	12.6	.93	1.91	.97
III	3	14	16	15.3	15	18	16.3	1.00	1.12	1.06
IV	32	15	19	16.1	17	24	19.9	1.13	1.44	1.24
V	29	17	28	19.5	14	34	28.6	1.30	1.67	1.47
VI	28	19	61	25.4	31	107	38.8	1.55	1.96	1.53
VII	21	22	39	27.2	38	68	55.0	1.65	2.26	2.02
VIII	26	24	55	27.8	53	87	65.2	2.14	2.60	2.34
IX	47	20	73	33.0	53	108	88.8	2.31	3.34	2.69
X	65	21	81	36.1	75	270	116.3	2.59	3.57	3.22
XI	149	22	98	44.1	81	378	180.0	3.21	5.38	4.09
XII	105	32	110	59.1	160	614	296.7	4.28	5.90	5.02
XIII	31	34	102	68.1	210	794	488.2	5.77	7.94	6.58

Increase in intestinal development then has meant the gradual acquirement in the first half year of life, of a relatively long intestine, as seen in the regular increase in ratios between intestine and fish lengths for successive stages of this development. (Table 2).

[4]The minimum (or maximum) ratios are not to be understood as belonging to the particular minimum (or maximum) lengths of fish, in any stage. Body lengths, intestinal lengths, and ratios, are independent in that sense. Small young fish, say of stage XII, have the same range of ratios as large old ones, of same stage. For instance, in stage XIII, the smallest fish (34 mm.), has a ratio of 6.17, and the largest fish (102 mm.), has a ratio of 6.58, both fairly near the average. Sometimes smallest fish happened to have unusually high ratios. In stage XII, the very smallest fish (32 mm.), has ratio 5.90, the maximum found for that stage, while the largest fish (110 mm.) has a ratio 5.53.

[5]The average ratio (and similarly for all average lengths given) is the actual average of all individuals in the stage, not merely between the minimum and maximum specimens.

If one expects less range in ratios for a stage, with no overlapping of those of successive stages, assuming that for each fish length the intestine lengths in one stage of development ought to be the same, it must be recalled that such close correlation cannot be expected. Length may either outstrip or fall behind growth or development of intestine. Amount of available food of proper sort must be a factor determining increase in length and bulk. In a few specimens, of average normal size, from a small creek collection early in summer, there was almost no increase in length after being kept in an aquarium for two months. Out in nature the growth was continuous and considerable during the same time, as shown by measurements of average size fishes at later collections. Nevertheless in these stunted aquarium specimens, of which, however, only two survived until this point was investigated, intestinal development had continued to quite the normal advanced stage.

Another matter of practical importance in overlapping of ratios, is the fact that many specimens are naturally somewhat intermediate in development, that is, between successive stages. All things considered the correlation is as high as could be reasonably expected, and the increase in relative intestine length is regular.

If all adult specimens be compared a considerable range in ratios would be noted. Forbes and Richardson (1920, p. 111), say: "Intestine 5 to 9.5 times length of head and body." Others have given similar figures. The present work shows that all fishes of stage XII yield the average ratio 5.02. Since the general ratio does not increase for older, larger fish in this stage, the figure might do for adults, and numerous adults could be selected from the collections in which the intestine would be no longer than five times the body length. For stage XIII, where maximum intestinal length has been developed, the number of times the intestine is longer than the body ranges from 5.77 to 7.94, with an average of 6.58, but only seven out of 31 specimens had an intestine over seven times the length of the body.

IV. Variations in Intestinal Coiling.

A small proportion of *Campostoma anomalum* show marked variation from the described, typical intestinal development. Minute deviations are not counted in as variations. Out of 543 specimens of table 2, 103 could be differentiated at least in some details of the outer coiling, but these cannot be of the least significance and they allow the specimens to be placed in a regular stage of intestinal development. Some (Plate VI, Figs. 68, 69), differ in appearance, due to slightly altered bends on the left side. In a few (Plate VI, Figs. 70, 72, 75), the dorsal side of the air bladder is not wholly covered posteriorly.

Some show so much variation that they cannot be homologized with the typical development. Most irregulars were characterized by absence of dorsal intestinal coiling, a noteworthy feature, in view of the usual coiling dorsally around air bladder. Out of 41 irregulars, 29 lacked all dorsal coiling, and were at same time old and large enough to have had it developed, were they typical. Only four very irregular specimens had some dorsal coiling, but they were otherwise so different as to have no similarity to the typical kind. The remaining 8 of the 41 were young, and naturally also without dorsal coiling, but they were so irregular otherwise that no direct comparison could be made with typical young. Apparently cases of irregular coiling begin very early in intestinal growth.

A number of specimens lacking dorsal coiling are figured, (Plate V, Fig. 63; Plate VI, Figs. 82, 87). The coiling, covering all other sides, has all main loops longitudinal, and this includes small subsidiary bends in the main longitudinal loops, chiefly on the ventral side. (Plate V, Fig. 61; Plate VI, Figs. 71, 80, 85). The left side shows in most cases long, sweeping bends, (Plate V, Figs. 60, 66; Plate VI, Figs. 79, 83, 84), and rarely a more straightened arrangement, (Fig. 76). The right side has in many cases two longitudinal coils, but one smaller than the other, (Plate V, Fig. 62; Plate VI, Fig. 81). The peculiar nature of this irregular coiling is best seen in view (Plate V, Fig. 64), of the entire turns flattened out as in (Plate IV, Fig. 46), with all essential bends retained. One of the very young of irregular type is similarly shown, (Plate V, Fig. 65).

The lack of dorsal coiling, though exceptional, is frequent and striking enough, so that one cannot safely make dorsal coiling around air bladder the main diagnostic test for the genus, as is done in most classification keys. In Pimephales promelas there is an arrangement markedly similar to many of these irregular Campostoma. The tpical, transverse Campostoma coiling is probably a specialized condition, and its absence may be thought of as a departure from the specialized method of the genus to a more generalized, earlier type of long intestine coiling.

On the basis chiefly of alimentary canal differences, Haseman (1906, p. 161) described a new species, *Campostoma brevis.* He compared an 81.5 mm. *C. anomalum* with an 83 mm. cotype of *C. brevis.* Measurements and descriptive details differ only minutely, having no significance and occurring within the range of variation of *C. anomalum*, but one distinct difference is an intestine in *brevis* scarcely half as long as in *anomalum.* His would yield a ratio of 4.41, intestine to body length, for *anomalum* as compared with 1.83 for *brevis.* Probably he did not measure in the apparent stomach, which would raise the *brevis* ratio well above two.

The writer found no 82 mm. or similar *anomalum* with nearly so short an intestine as in this *brevis.* All those lacking dorsal coiling had somewhat shorter intestine than typical ones of same size, but the difference was usually small.

There are other respects in which intestine of my irregular specimens, is either like the described *brevis*, or even more different than it, from typical *anomalum.* The writer would not consider making a new species for even the most irregular intestine type. Many of these in fact were found closely associated with a group of those shown to have regular coiled intestine, so that they must have belonged to the same school of young.

He gives among other intestine features, a diameter of 1.5 to 2 mm. for *brevis*, compared with 1 mm. for *anomalum.* The latter have a 1 mm. diameter average for such size fishes (omitting of course the swollen part). But one specimen, 74 mm. long, (Plate VI, Fig. 86), has intestines fully 2 mm. thick throughout. This intestine appears very short, but still having a ratio of 2.66, is longer than that of the described *brevis.*

Haseman says: "The alimentary canal of *brevis* does not go around the air bladder more than one or two times; and the other folds are not spiral, but longitudinal." The specimen referred to (Fig. 86), like *brevis* in its thick canal, does not have even one coil around the air bladder; and a total of 29 irregular specimens lack all dorsal coiling, and have it entirely longitudinal. A sort of intermediate specimen, (Plate VI, Fig. 70), has merely a few coils around; however it has a very long intestine.

He described for *brevis* a white intestine, less fragile than the dark one of *anomalum*. *Anomalum* intestine is a dark, greenish brown in color, but several nearly white intestines were found, which was due to their possessing a much thicker wall. (Plate V, Fig. 66, was one of these). They were among those lacking all dorsal coiling, but the intestine was of small diameter and great length. He calls *anomalum* a mud-eater, and says *brevis* also has some "grassy substance" in its canal. *Anomalum* contents are mixed inorganic and organic matter, the latter largely diatoms, but there may be more or less green matter. (Kraatz, 1923). A very few had fed on green algæ exclusively, but they were darker, not lighter, and more fragile, rather than less.

While no positive statement can be made, the discussion shows that various more or less irregular specimens of *C. anomalum* show one or more of the various distinguishing *C. brevis* features, and that all sorts of variations and gradations occur, so that there seems insufficient basis, even with so short an intestine, for a new species.[6]

V. Relation of Intestine to Adjacent Structures.

Liver.

The liver is large, filling up space adjacent to the anterior parts of the intestinal mass.

On the left in all specimens, (Plate VII, Fig. 92), liver occupies all space in front of the most anterior, inverted, U-shaped bend of the intestine, and dorsal to it, and also in front of the double-U-shaped bend (c-e). In a few cases it does not extend as far back. The liver is rounded off anteriorly. From this large left lobe a narrow flat lobe extends and attenuates posteriorly, beneath the intestinal coils, which, as they develop around it, press grooves upon this liver lobe.

The large liver mass continues around ventrally and up the right side (Fig. 93), filling the larger space there, formed by the intestinal loops passing from the left diagonally and therefore more posteriorly to the right. From this large right lobe a thin

[6]Mr. Carl L. Hubbs, who subsequently examined *C. brevis* types, says it does not form a new species.

lobe extends tongue-like posteriorly, describing a long spiral of more than half a turn counter clockwise around the air bladder, and completely covered up by intestinal coils.

There are some variations in size and arrangement of liver, but these can be of no significance, and are dependent upon variations in arrangement of intestinal loops. Only the typical form has been figured.

Gall Bladder.

The gall bladder is a small dorsal sac appended to the alimentary canal by a fine duct, somewhat behind the middle of the anterior canal section. The point of junction is not always in relatively the same place. The sac folds down anteriorly, is covered with fatty tissue, but is not embedded in liver. It is shown in practically normal position, (Plate VII, Fig. 89), with the ducts slightly raised. The other illustrations (Figs. 88, 90, 91), show it swung up free from the canal, in Fig. 88 up around to the right of the ducts. The gall bladder is practically always of very similar form and fairly uniform size.

The cystic duct is short and straight, and about one-third the length of the bladder itself. The common bile duct or choledochal duct is three times as long as the cystic duct. Its lower part is rather close to and parallel to the intestine, and the exact place of entrance is rather hard to make out. It is not dorsal but on the left side.

The hepatic ducts were not studied much. Either one duct or two ducts come off from the common bile duct and diverge from the cystic duct. Wherever there was but one this soon divided into two branches, which entered the liver, apparently the right lobe, which extends around the air bladder. In rare cases three hepatic ducts were seen to come off together at the cystic duct junction. Just within the liver tissue the hepatic ducts divide into a number of smaller branches.

Pancreas.

The pancreas is difficult to distinguish. The following account is merely a preliminary statement.

In a considerable number of specimens examined, a fine irregular diffuse tissue, arranged lengthwise on the dorsal side, on the posterior half of the intestinal canal section, seemed likely to be pancreas. No ducts were found leading into intestine, but under low power of the microscope some specimens showed masses of finely branched lobulated tissue with some fine tubules. Such a diffuse condition would not be unusual for fish pancreas.

It is also possible that pancreatic tissue may be included in liver, so that this organ would be an hepato-pancreas, which is not unusual in fishes. Oppel (1896, p. 42), gives, after Krukenberg, (1882), in a table of distribution of digestive glands and enzymes, an hepato-pancreas present for all Cyprinidæ.

The striking variability in condition of pancreas among fishes is well stated by Kerr (1919, Vol. II, p. 190). About *Campostoma* no conclusion can naturally be made without an extensive study histologically of pancreas and liver.

Gonads.

The gonads lie dorsal to the coiled intestinal mass, and are not enclosed in the coils, though it has been said, (Jordan and Evermann, 1896, p. 294): "ovaries similarly enclosed by the alimentary canal." If the oviduct were enclosed it would be compressed by intestinal coils, especially where there are both inner and outer coils, and most in later stages. Even anteriorly where there are no inner loops, the intestine presses upon the enclosed liver to make depressions upon it. It would seem impossible for an ovary to have room to develop within the coils anywhere.

Ovaries were observed in many specimens, but most were immature. Young specimens of not over 40 mm. (Plate VII, Fig. 98), had such immature ovaries. Nothing is known of rate of ovary development. A few specimens considerably larger and further developed in other organs possessed, nevertheless, an ovary of small size, (Fig. 99). An older ovary (Fig. 100), fills up more space laterally and dorsally to the anterior half of the intestinal mass, including available space above the air bladder not filled by intestine. In this condition the two ovaries were found to be identical, and nearly touched along the median dorsal line.

In much older specimens the ovary is considerably larger, (Plate VII, Figs. 101, 102). These figures show the largest specimen at hand having a much larger ovary than in above-described stages. Only one other specimen, (smaller in size), had what seemed a fully developed ovary, and it was exactly like the other, so that the one here treated of seems likely to be a normal adult form of ovary.

In this the ovary covers most of the intestinal mass on the left side. Only the inverted U-shaped bends are exposed anteriorly, and it extends in somewhat beneath these, (Fig. 102). The ovaries have lost symmetry, and are not bilaterally placed. The right is larger and has somehow come to be placed dorsally. It also extends down on the left, its lower margin making a diagonal line passing to the ventral side at the posterior end. Only at the anterior end above the liver, does the right ovary occupy the right side. Why the right ovary should not pass backward on the right over intestine is not clear, since it does push over dorsally and down the left side. The left lobe is smaller. Its upper margin adjoins the lower margin of the right ovary, (Fig. 101). It is pushed somewhat ventrally by the right one, but does not extend farther than the mid-ventral line.

VI. Summary.

Campostoma anomalum normally has its air bladder (except dorsally at anterior end) encircled by many loops of a transversely coiled intestine, a feature found only in this genus of fishes.

The species is similar in most essential respects to other Cyprinidæ, in lacking a true functional stomach, a conclusion based on various features of canal structure different from those of Teleosts, having a true stomach.

The mucosa lining bears zig-zag, lengthwise folds. The zig-zag ridges are comprised of columns of Vs, which become smaller posteriorly. Farther back parts of the Vs disappear, merely short ridge pieces remaining, while at the end all folds are lacking.

In the very young fish, the canal, between oesophagus and anus, consists of three straight portions (anterior, middle, posterior), in a flattened Z shape. The anterior swollen portion is the apparent stomach.

Adult intestinal condition is the result of regular increase of coiling during the first year of growth. The first growth, a U-shaped bend, at anterior end of posterior canal section, plus another bend in the middle canal section, form a double U, the elongation of the rounded end of which, pushing counter clockwise around the air bladder, produces most of the intestinal coiling. Either two and one-half or sometimes three complete turns occur. There is a similar, shorter inner growth at the end of the anterior canal section, and also a lengthening of the posterior section by simple spiral growth.

The number of times the intestine is longer than the body increases with the stage of development. In many developed specimens it is 5 times, and in some few 6 and even more than 7 times the length of the body.

There are some irregular specimens, (one-fourteenth of all those studied) which for the most part lack all dorsal coiling and are thus very atypical in intestinal plan.

The liver occupies available space anteriorly in the abdominal cavity, and has thin lobes extending posteriorly, which are covered by intestinal coils. The gall bladder is a dorsal sac attached somewhat behind the middle of the anterior canal section.

The ovaries are not enclosed by the coiled intestinal canal, but lie directly upon it.

EXPLANATION OF PLATES.

All Figures illustrating intestinal development (Plates I–V), show alimentary canal posterior to oesophagus, and include also the air bladder. So as not to obstruct clear view of intestinal coils, all liver, mesentery, fat, gonads, etc., are omitted. Fine, parallel lines indicate air bladder, distinguishing it from intestine which is stippled.

Plate I.

All Figures × 2 & 2/3.

Fig. 1. Stage I, left view, specimen No. 296, length 14 mm.
Fig. 2. Stage I, ventral view, specimen No. 296, length 14 mm.
Fig. 3. Stage II, left view, specimen No. 299, length 13 mm.
Fig. 4. Stage II, ventral view, specimen No. 299, length 13 mm.
Fig. 5. Stage III, left view, specimen No. 365, length 16 mm.
Fig. 6. Stage III, ventral view, specimen No. 365, length 16 mm.
Fig. 7. Stage IV, left view, specimen No. 314, length 16 mm.
Fig. 8. Stage IV, ventral view, specimen No. 314, length 16 mm
Fig. 9. Stage IV, right view, specimen No. 314, length 16 mm.
Fig. 10. Stage V, left view, specimen No. 367, length 18.5 mm.
Fig. 11. Stage V, ventral view, specimen No. 367, length 18.5 mm.
Fig. 12. Stage V, right view, specimen No. 367, length 18.5 mm.
Fig. 13. Stage VI, left view, specimen No. 383, length 24 mm.
Fig. 14. Stage VI, ventral view, specimen No. 383, length 24 mm.
Fig. 15. Stage VI, right view, specimen No. 383, length 24 mm.
Fig. 16. Stage VII, left view, specimen No. 401, length 26 mm.
Fig. 17. Stage VII, ventral view, specimen No. 401, length 26 mm.
Fig. 18. Stage VII, right view, specimen No. 401, length 26 mm.
Fig. 19. Stage VIII, left view, specimen No. 396, length 25 mm.
Fig. 20. Stage VIII, ventral view, specimen No. 396, length 25 mm.
Fig. 21. Stage VIII, right view, specimen No. 396, length 25 mm.

Plate II.

All Figures × 2 & 2/3.

Fig. 22. Stage VII, dorsal view, specimen No. 401, length 26 mm.
Fig. 23. Stage VIII, dorsal view, specimen No. 396, length 25 mm.
Fig. 24. Stage IX, dorsal view, specimen No. 422, length 28 mm.
Fig. 25. Stage IX, left view, specimen No. 422, length 28 mm.
Fig. 26. Stage IX, ventral view, specimen No. 422, length 28 mm.
Fig. 27. Stage IX, right view, specimen No. 422, length 28 mm.
Fig. 28. Stage IX, spread out flat, specimen No. 422, length 28 mm.
Fig. 29. Stage X, left view, specimen No. 522, length 37 mm.
Fig. 30. Stage X, ventral view, specimen No. 522, length 37 mm.
Fig. 31. Stage X, right view, specimen No. 522, length 37 mm.
Fig. 32. Stage X, dorsal view, specimen No. 522, length 37 mm.

Plate III.

All Figures × 2.

Fig. 33. Stage XI, left view, specimen No. 195, length 41 mm.
Fig. 34. Stage XI, ventral view, specimen No. 195, length 41 mm.
Fig. 35. Stage XI, dorsal view, specimen No. 195, length 41 mm.
Fig. 36. Stage XI, right view, specimen No. 195, length 41 mm.
Fig. 37. Stage XI, spread out flat, specimen No. 195, length 41 mm.
Fig. 38. Stage XI, inner coils only, specimen No. 195, length 41 mm.
Fig. 39. Stage XI, variation inner coil, specimen No. 485, length 39 mm.
Fig. 40. Stage XI, variation inner coil, specimen No. 133, length 37 mm.
Fig. 41. Stage XI, variation inner coil, specimen No. 589, length 30 mm.
Fig. 42. Stage XII, left view, specimen No. 151, length 48 mm.
Fig. 43. Stage XII, ventral view, specimen No. 151, length 48 mm.

Plate IV.

All Figures × 2.

Fig. 44. Stage XII, right view, specimen No. 151, length 48 mm.
Fig. 45. Stage XII, dorsal view, specimen No. 151, length 48 mm.
Fig. 46. Stage XII, spread out flat, specimen No. 151, length 48 mm.
Fig. 47. Stage XII, inner coils, specimen No. 151, length 48 mm.
Fig. 48. Stage XII, variation inner coil, specimen No. 238, length 44 mm.
Fig. 49. Stage XII, variation inner coil, specimen No. 206, length 50 mm.
Fig. 50. Stage XII, variation inner coil, specimen No. 594, length 39 mm.
Fig. 51. Stage XII, variation inner coil, specimen No. 597, length 36 mm.
Fig. 52. Stage XII, variation inner coil, specimen No. 17, length 41 mm.
Fig. 53. Stage XII, variation inner coil, specimen No. 221, length 54 mm.
Fig. 54. Stage XII, variation inner coil, specimen No. 583, length 36 mm.
Fig. 55, Stage XIII, inner coil, specimen No. 123, length 49 mm.

Plate V.

All Figures × 2.

Fig. 56. Stage XIII, left view, specimen No. 123, length 49 mm.
Fig. 57. Stage XIII, ventral view, specimen No. 123, length 49 mm.
Fig. 58. Stage XIII, right view, specimen No. 123, length 49 mm.
Fig. 59. Stage XIII, dorsal view, specimen No. 123, length 49 mm.
Fig. 60. Irregular coiling, left view, specimen No. 58, length 42 mm.
Fig. 61. Irregular coiling, ventral view, specimen No. 58, length 42 mm.
Fig. 62. Irregular coiling, right view, specimen No. 58, length 42 mm.
Fig. 63. Irregular coiling, dorsal view, specimen No. 58, length 42 mm.
Fig. 64. Irregular coiling, spread out flat, specimen No. 58, length 42 mm.
Fig. 65. Irregular coiling, spread out flat, specimen No. 393, length 24 mm.
Fig. 66. Irregular coiling, left view, specimen No. 270, length 60 mm.

Plate VI.

Photographs. All Figures × 1.

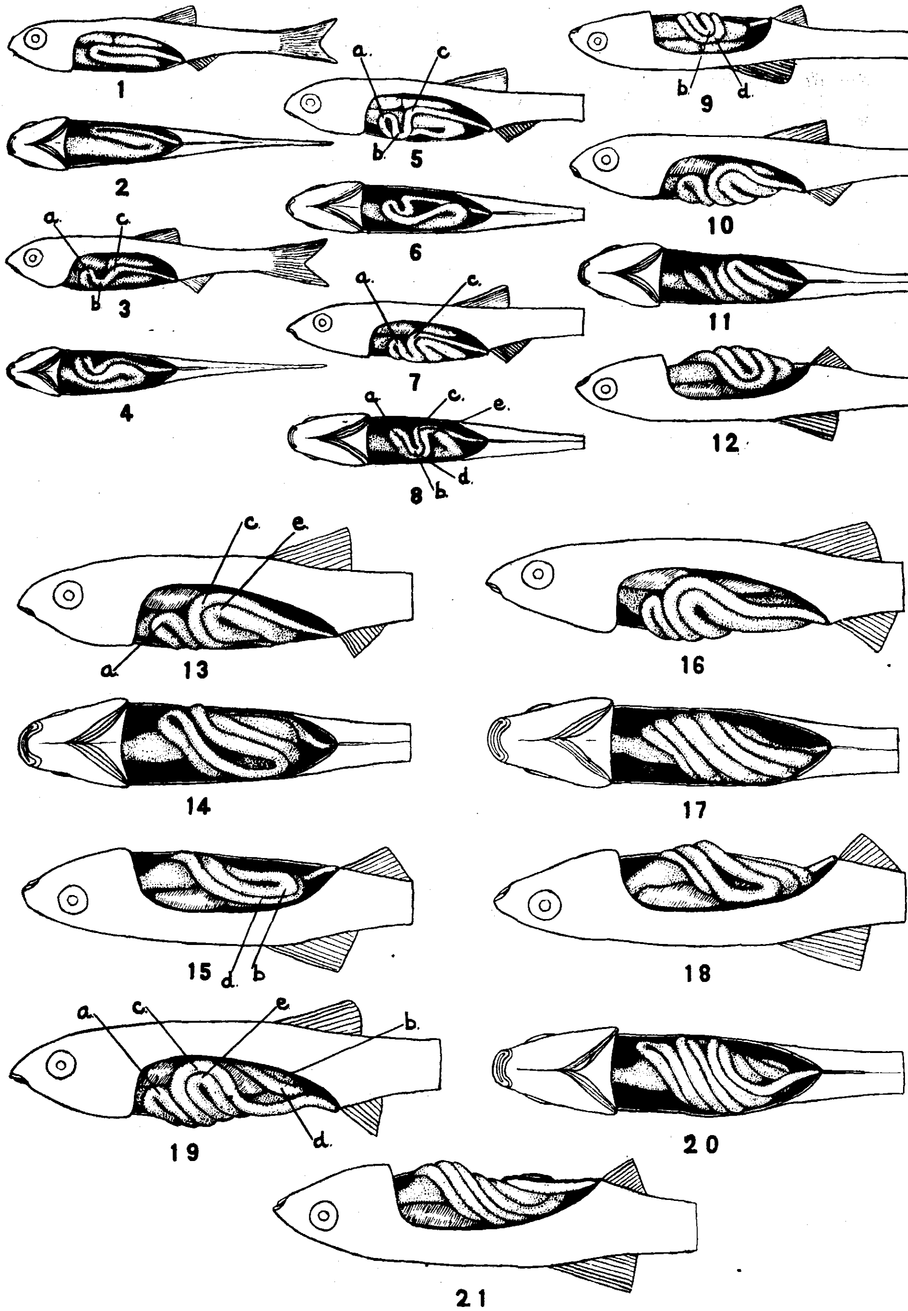
Fig. 67. Typical coiling, left view, specimen No. 13, length 36 mm.
Fig. 68. Somewhat atypical, left view, specimen No. 252, length 100 mm.
Fig. 69. Somewhat atypical, ventral view, specimen No. 252, length 100 mm.
Fig. 70. Somewhat more atypical, left view, specimen No. 552, length 71 mm.
Fig. 71. Somewhat more atypical, ventral view, specimen No. 552, length 71 mm.
Fig. 72. Somewhat more atypical, left view, specimen No. 108, length 71 mm.
Fig. 73. Somewhat more atypical, ventral view, specimen No. 108, length 71 mm.
Fig. 74. Somewhat more atypical, right view, specimen No. 108, length 71 mm.
Fig. 75. Somewhat more atypical, dorsal view, specimen No. 108, length 71 mm.
Fig. 76. Irregular coiling, left view, specimen No. 572, length 59 mm.
Fig. 77. Irregular coiling, ventral view, specimen No. 214, length 86 mm.
Fig. 78. Irregular coiling, left view, specimen No. 51, length 66 mm.
Fig. 79. Irregular coiling, left view, specimen No. 111, length 57 mm.
Fig. 80. Irregular coiling, ventral view, specimen No. 111, length 57 mm.
Fig. 81. Irregular coiling, right view, specimen No. 111, length 57 mm.
Fig. 82. Irregular coiling, dorsal view, specimen No. 111, length 57 mm.
Fig. 83. Irregular coiling, left view, specimen No. 35, length 56 mm.
Fig. 84. Irregular coiling, left view, specimen No. 43, length 63 mm.
Fig. 85. Irregular coiling, ventral view, specimen No. 43, length 63 mm.
Fig. 86. Irregular coiling, left view, specimen No. 65, length 74 mm.
Fig. 87. Irregular coiling, dorsal view, specimen No. 65, length 74 mm.

Plate VII.

Fig. 88. Gall bladder and ducts; Ga, gall bladder; Cy, cystic duct; He, hepatic ducts; Ch, choledochal or common bile duct. The gall bladder is lifted up dorsally. Specimen No. 48, length 36 mm. × 4.
Fig. 89. Gall bladder and ducts; same fish but with bladder in natural position. × 4.
Fig. 90. Gall bladder and ducts. Specimen No. 228, length 46 mm. × 4.
Fig. 91. Gall bladder and ducts. Specimen No. 240, length 42 mm. × 4.
Fig. 92. Liver, shown in relation to air bladder; no intestine shown; length 49 mm. Left view, × 2.
Fig. 93. Liver, from same fish, right view, × 2.
Fig. 94. Intestinal mucosa surface; anterior part of swollen region. Longest dimension of drawing is in circular surface of mucosa, spread out flat; shorter dimension is in direction of length of intestine. The grooves are shaded. Specimen No. 253, length 95 mm. × 6.
Fig. 95. Intestinal mucosa surface; part of swollen region somewhat anterior to common bile duct junction. In same position and from same fish as Fig. 94. × 6.
Fig. 96. Intestinal mucosa surface; farther posteriorly, about half way back to anus. Same position and from same fish as Fig. 95. × 6.
Fig. 97. Intestinal mucosa surface; portion still farther posteriorly, about half way between Fig. 96 and anus. Same position and from same fish. × 6.
Fig. 98. Ovary. Left side; specimen No. 25; length 39 mm. × 2.
Fig. 99. Ovary. Left side; specimen No. 145; length 73 mm. × 2.
Fig. 100. Ovary. Left side; specimen No. 276; length 58 mm. × 2.
Fig. 101. Ovary. Left side; specimen No. 290; length 80 mm. × 2.
Fig. 102. Ovary. Dorsal view, showing the right ovary; specimen No. 290; × 2.

The Intestine of Campostoma,
Walter C. Kraatz.

PLATE I.



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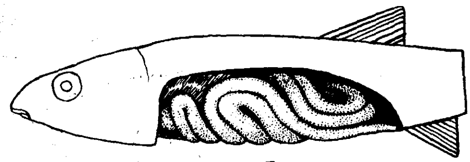

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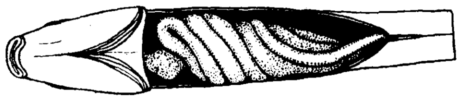

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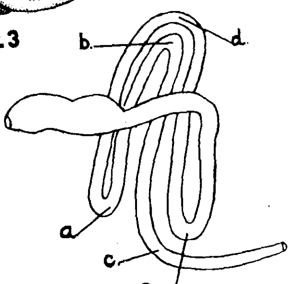

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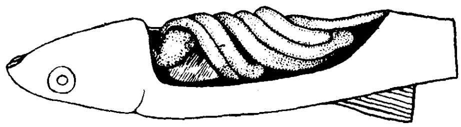

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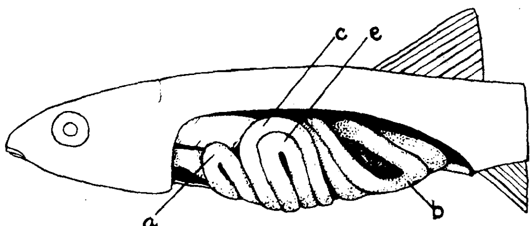

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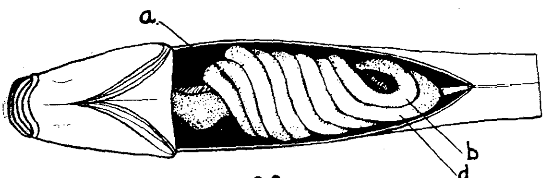

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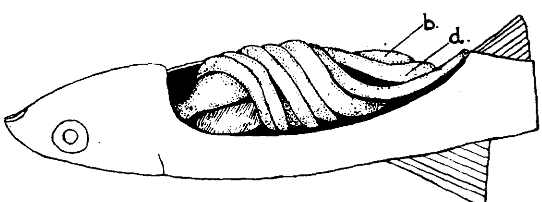

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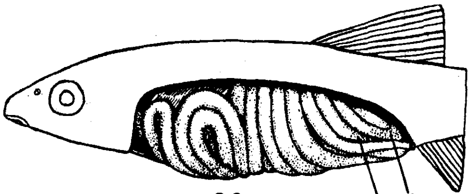
The Intestine of Campostoma,
Walter C. Kraatz.

PLATE III.



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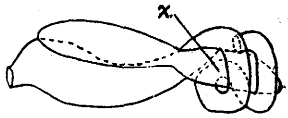

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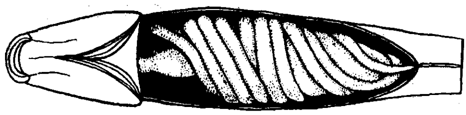

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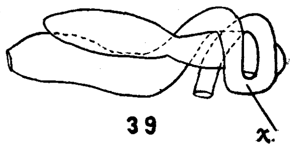

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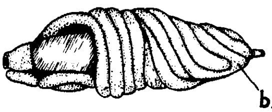

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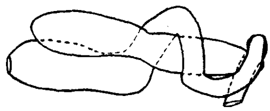

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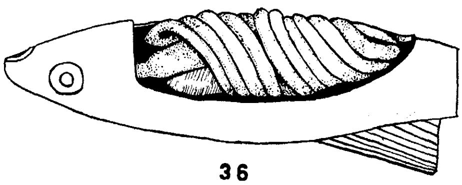

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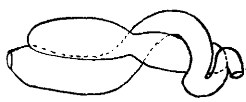

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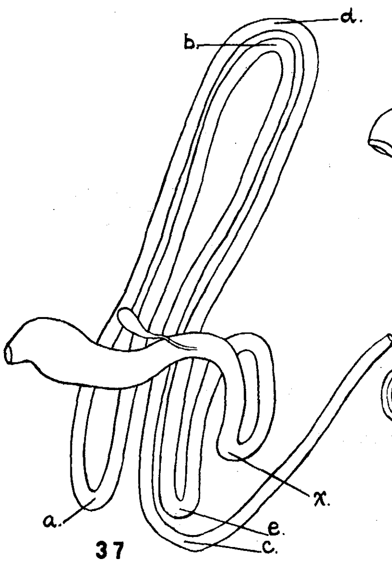

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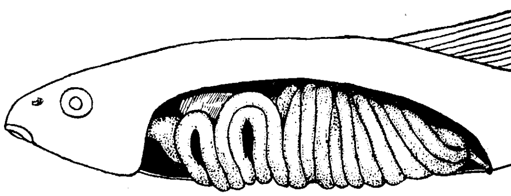

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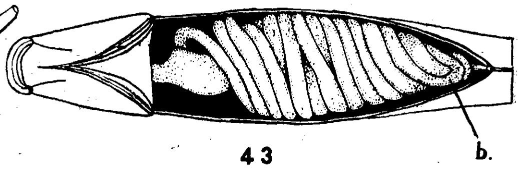

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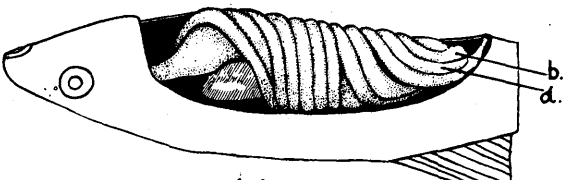

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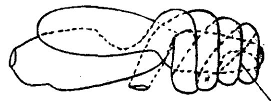

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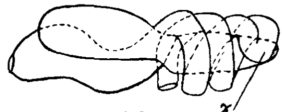

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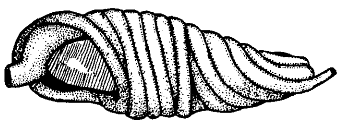

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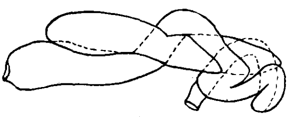

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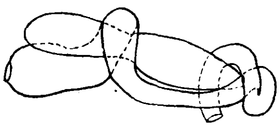

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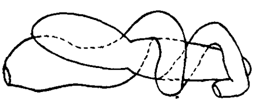

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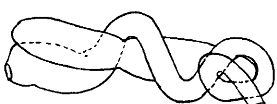

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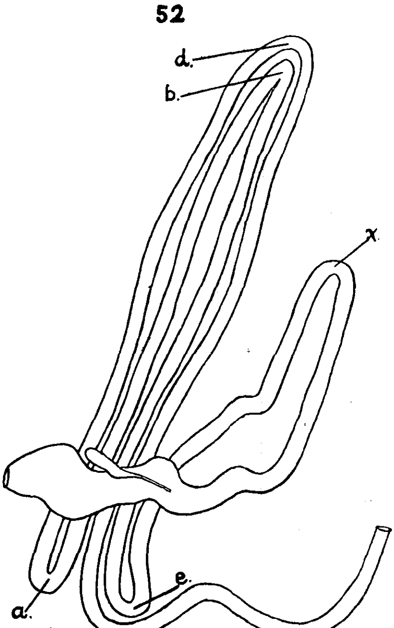

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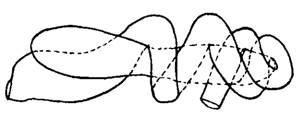

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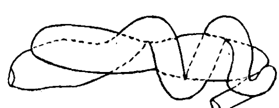

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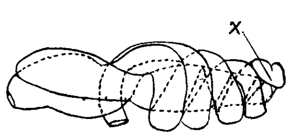

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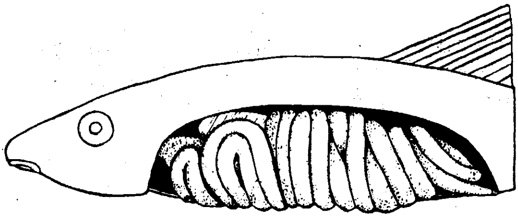

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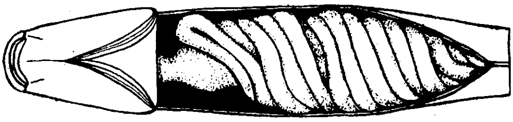

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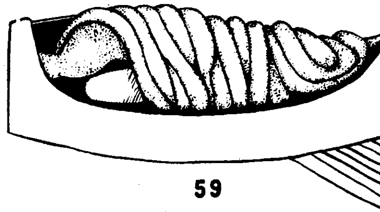

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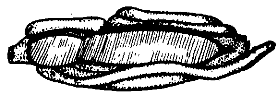

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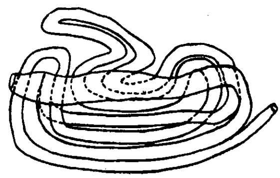

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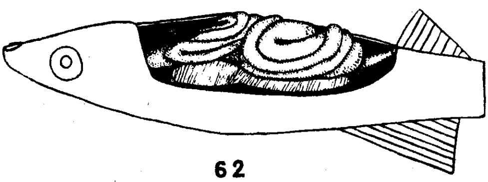

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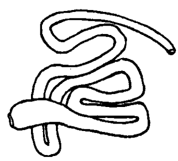

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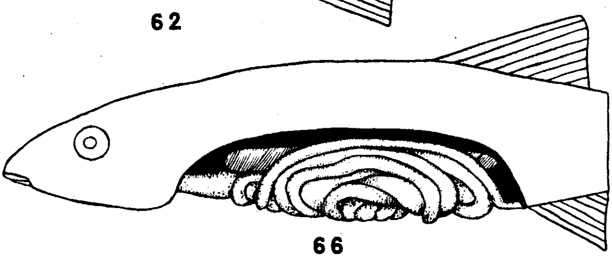

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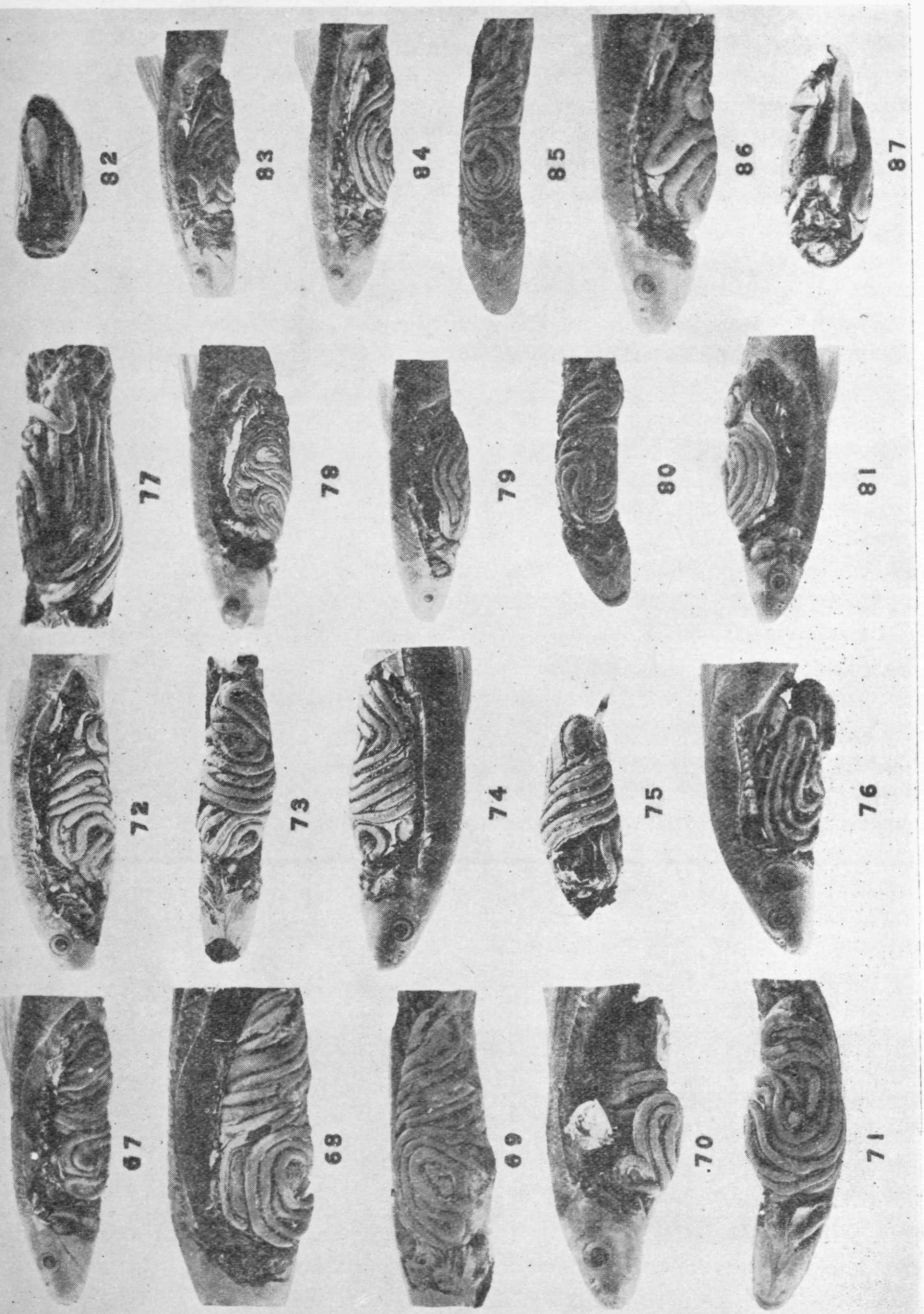
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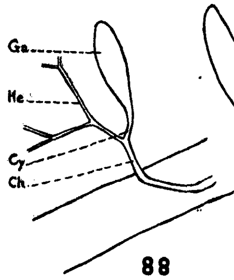

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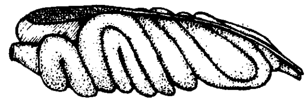

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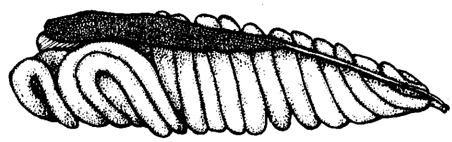

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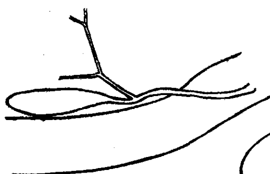

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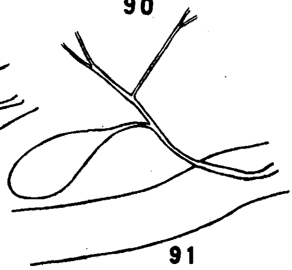

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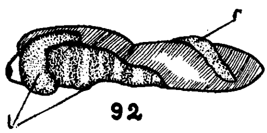

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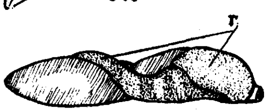

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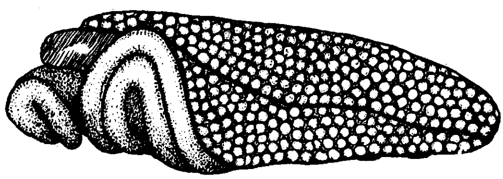

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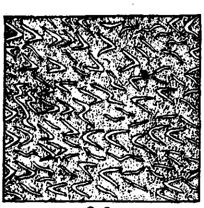

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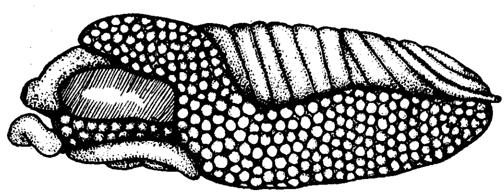

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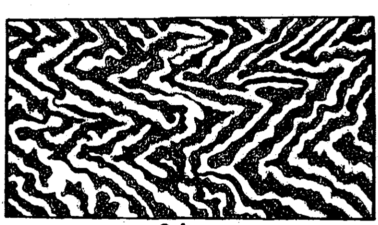

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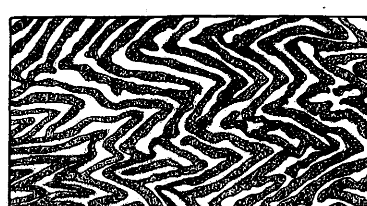

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BIBLIOGRAPHY.[7]

AGASSIZ, L.
1855. Campostoma anomalum. Amer. Jour. Sci. & Arts, p. 218.

BIEDERMAN, W.
1875. Untersuchungen uber das Magenepithel. Sitzung. Wiener Akad. Vol. LXXI, No. 3-5, pp. 377-398.

BISCHOFF, T. W. L.
1838. Uber den Bau der Magenschleimhaut. Mullers Archiv fur Anat. und Physiol., pp. 503-525.

BREDER, C. M. JR., AND CRAWFORD, D. R.
1922. The food of certain minnows, a study of the seasonal dietary cycle of six cyprinoids, with special reference to fish culture. Zoologica, Vol. II, No. 14, pp. 287-327.

BRINTON, W.
1854. Stomach and intestine. Todd's Encyclop. Vol. I, pp. 293-423.

CATTANEO, G.
1886. Sull 'existenza delle glandule gastriche, nell 'Acipenser sturio e nelle Tinca vulgaris. Rend. Reale Instituto Lomb. di scienze e lettre, Ser. II, Vol. XIX, pp. 676-682.

COX, U. O.
1897. A preliminary report on the fishes of Minnesota. Geol. & Nat. Hist. Surv. Minn., Zool. Ser. III, pp. 1-93.

CREVECOEUR, F. F.
1907. A new species of Campostoma? Kans. Kans. Acad. Sci., Vol. 21, No. 1, pp. 155-157.

DECKER, FR.
1887. Zur Physiologie des Fischdarmes. Festschrift fur A. v. Kolliker, pp. 387-411.

EDINGER, LUDWIG.
1877. Uber die Schleimhaut des Fischdarmes, nebst Bemerkungen zur Phylogenese der Drusen des Darmrohres. Archiv. fur Mikro. Anat., Vol. XIII.

FORBES, S. A., AND RICHARDSON, R. E.
1908. The fishes of Illinois. Ill. State Lab. Nat. Hist. (2nd ed., 1920), pp. 1-cxxv, & 1-357.

GAREL, J.
1879. Recherches sur L. 'antomie generale comparee et la signification morphologiques des glands de la muquesse intestinale et gastrique des animaux vertebres. Lab. d'Anat. gen de la. Fac. Med. de Lyon, Paris.

GEGENBAUR, C.
1878. Bemerkungen uber den Vorderdarm niederer Wirbeltiere. Morphol. Jahr., Vol. IV, pp. 314-319.

HANKINSON, T. L.
1919. Notes on the life history of Illinois fishes. Trans. Ill. Acad. Sci., Vol. XII, pp. 132-150.

HASEMAN, J. D.
1906. Campostoma brevis. Proc. Ind. Acad. Sci., pp. 161-165.

JORDAN, D. S.
1905. A guide to the study of the fishes. Henry Holt & Co. Vol. I, pp. 1-624; Vol. II, pp. 1-599.

[7]For a much more complete bibliography on anatomoical and physiological phases of fish digestive system, the works of Oppel (1896, 1897), Yung (1899), and Wiedersheim (1907), should be consulted. The most useful and available American keys and papers giving information on *Campostoma* are included in this list.

JORDAN, D. S., AND EVERMANN, B. W.
1896. The fishes of North and Middle America. Bull. U. S. N. M., No. 47, 4 Vols. (see Vol. I, pp. 204-206; and Vol. IV, p. xv, & p. 3207).

KERR, J. GRAHAM.
1919. Text book of embryology. Macmillan & Co., London. Vol. II, pp. 1-591.

KINGSLEY, J. S.
1912. Comparative anatomy of Vertebrates. Blakison's Son & Co., pp. 1-401.

KRAATZ, W. C.
1923. A study of the food of the minnow Campostoma anomalum. Ohio Jour. Sci., Vol. XXIII, pp. 265-283.

KRUKENBERG, C. F. W.
1877. Versuche zur vergleichende Physiologie der Verdauung mit besonder Berucksichtigung der Verhaltnisse bei den Fischen. Unter. d. Phy. Inst. der Univ. Heidelberg, Bd. I, pp. 327-240.

LUCHHAU, ERNST.
1878. Uber die Magen- und Darmverdauung bei einigen Fischen. Konigsberg, Inaug. Diss., pp. 1-28.

MECKEL, J. F.
1829. System der vergleichenden Anatomie. 4 teil. Halle.

OPPEL, A.
1896. Lehrbuch der vergleichenden mikroskopischen Anatomie der Wirbeltiere. Band I. Magen., Jena, pp. 1-543.
1897. Ibid. Band. II. Schlund und Darm.

OSBURN, R. C.
1901. The fishes of Ohio. Ohio State Acad. Sci., Spec. Paper No. 4, pp. 1-104.

PICTET, ARNOLD.
1909. Contribution histologique du tube digestif des poissons cyprinoides. Rev. Suisse de Zool., Annal. Soc. Zool. Suisse et Mus. Hist. Nat., Vol. 17, pp. 1-79.

RADTHKE, H.
1837. Zur Anatomie der Fische. Mullers Archiv fur Anat. & Physiol., Vol. I, pp. 335-356.

SMITH, HUGH M.
1907. The fishes of North Carolina. N. Car. Geol. & Econ. Surv., Vol. 2, pp. 1-453.

VALATOUR, MARTIAL.
1861. Recherches sur les glandes gastriques et les tuniques musculaires du tube digestif dans les Poissons osseux et les Batraciens. Annal. Sci. Nat., 4 serie, Zool. Vol. XVI, pp. 1-219.

WIEDERSHEIM, ROBERT.
1907. Elements of the comparative anatomy of Vertebrates. (trans. W. N. Parker). Macmillan Co., pp. 1-576.

YUNG, EMILE.
1899. Recherches la digestion des Poissons. (Histologie et physiologie de l'intestin). Archives Zool. Exper. et Gen., Paris. pp. 121-201.